

Long-term bird population studies in the United States

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Long-term population studies of birds in the United States have been less species-oriented and more concept-oriented than in Britain. The demographics of North American species do not differ grossly from those of species elsewhere in the world, but polygamy has been relatively more frequently studied in U.S. species than elsewhere. Subjects that have been particularly explored in long-term studies in the United States include the determinants of cooperative breeding in birds, the effects of the spatial scale on what is learned, and correlates of regional and national declines in bird populations. Other areas of developing interest include the potential uses of monitoring data, the relative value of longitudinal and cross-sectional studies in analysing slow processes, and the significance of episodic events in shaping population patterns.

As a broad generalization, British ornithology is rich in long-term population studies focused on individual species (Lack 1966). Studies on Fulmar *Fulmarus glacialis* (Ollason & Dunnet 1988), Kittiwake *Rissa tridactyla* (Coulson & Thomas 1985), Red Grouse *Lagopus lagopus* (Watson *et al.* 1984), Great Tit *Parus major* (Perrins 1979), and Grey Partridge *Perdix perdix* (Potts 1986), are particularly well-known examples, and others are discussed in this volume. Few studies of this type have become established in the United States, both absolutely and in relation to the number of ornithologists. The study by Nice (1937) on the Song Sparrow *Melospiza melodia* is the classic example of a long-term population study in North America, but few other species come immediately to mind, in contrast to Britain. U.S. studies that do share something of the characteristics of the studies cited above are those of Nolan (1978) on the Prairie Warbler *Dendroica discolor*, Oring & Lank (1982) on the Spotted Sandpiper *Actitis macularia*, Woolfenden & Fitzpatrick (1984) on the Florida Scrub Jay *Aphelocoma coerulescens*, Hamerstrom & Hamerstrom (1986) on the Northern Harrier *Circus cyaneus*, and Brown (1987) on the Mexican Jay *Aphelocoma ultramarina*. Other long-term population studies are being pursued in the United States, but most lack the species orientation of the classic British studies. (I note in passing that I am dealing here only with the United States and some exemplary studies elsewhere in North America, notably the long-term study of the Snow Goose *Chen caerulescens* on La Perouse Bay by Cooke and his co-workers (Healy *et al.* 1980) and the study of the Song Sparrow population on Mandarte Island, British Columbia (Smith 1988) would undoubtedly be discussed with a broader geographical remit.)

Table 1 summarizes various population parameters for species studied either in the United States or elsewhere, based on data compiled by Kulesza (1980). The similarity of parameter values in the two fairly large groups of species in Table 1 makes it unlikely that species studied in the United

States differ demographically from those studied elsewhere. In principle, long-term studies world-wide might involve species with demographic characteristics amenable to protracted study. However, as most of the studies in Table 1 are short-term ones and thus are less likely to be subject to a selective retention bias, I conclude that avian demographics in the U.S. and in Britain are fairly similar.

The similarity of parameters within the two groups in Table 1 does not preclude the possibility of there being some differences within particular ecological or taxonomic groups. For example, Dobson (1981) showed that North American long-distance migrants have higher survival than have their Palearctic counterparts, possibly because the latter have to traverse Mediterranean countries in which the hunting of songbirds is still permitted. Similarly, polygamy appears to be relatively more frequent in North American species than in Europe (see below).

Given the lack of basic demographic differences between birds in the United States and those elsewhere, trans-Atlantic differences in studies must reflect the choice of study species by individual researchers. North American ornithologists seem to be more concept-oriented than their British counterparts, choosing species because of their putative value in addressing previously identified scientific problems rather than choosing a species on which to work and developing the subsequently emergent conceptual topics. Since the theme of the present volume focuses on the *future* of long-term bird population studies, I develop here discussion only of those areas in which active research seems to be developing into new areas of general scientific interest.

In a recent review, Franklin (1989) noted that most American ecological studies have been very short-term (typically three years) in duration. However, he identified six areas of study in which long-term ecological research programmes could contribute uniquely. These included the study of slow processes, the effects of rare events or episodic phenomena, processes with high variability, subtle processes

	U.S. studies			Other studies			U-test
	Mean	s.d.	N	Mean	s.d.	N	
Total nest failure ¹	0.48	0.18	38	0.52	0.21	36	n.s.
Predation intensity ²	0.31	0.18	33	0.41	0.26	7	0.08
Clutch size	4.37	0.99	42	3.93	1.56	36	n.s.
Relative clutch weight ³	4.13	0.90	24	3.82	1.10	29	n.s.
Breeding attempts	1.79	0.64	21	3.22	2.01	9	n.s.
Productivity ⁴	2.99	1.65	22	3.73	2.37	10	n.s.
Adult mortality	0.47	0.10	18	0.45	0.14	22	n.s.

Table 1. Some demographic parameters from population ecology studies in the United States and elsewhere. Compiled from all data available in Kulesza (1980).

¹ Proportion of nests with eggs from which no fledglings were produced.

² Proportion of eggs subsequently predated as eggs or nestlings.

³ Clutch size times relative egg weight (= weight of egg divided by weight expected for a species of that body size).

⁴ Fledged young per female per season.

and complex phenomena, and the foundation and testing of ecological theory. Not all of these are immediately applicable to long-term population studies in birds, at least as at present conducted, but these concepts need eventual integration into the avian studies. For the present paper, I concentrate on just four topics, reflecting the most active areas of long-term bird studies in the United States. These are (a) the study of the demography of long-lived species, particularly in cooperative breeders, (b) the use of extensive monitoring data as the basis for studies complementing site-based longitudinal studies, (c) studies of spatial variation as a scale phenomenon, and (d) the study of slow or episodic processes.

DEMOGRAPHY OF LONG-LIVED SPECIES

Cooperative breeding

The study of cooperative breeding in birds has been a major field of sustained research in the United States, with long-term population studies directed at no less than six species—Florida Scrub Jay, Mexican Jay, Pinyon Jay *Gymnorhinus cyanocephalus*, Acorn Woodpecker *Melanerpes formicivorus*, Red-cockaded Woodpecker *Picoides borealis*, and Harris' Hawk *Parabuteo unicinctus*. General reviews of the subject have been provided by Emlen & Vehrencamp (1983) and Brown (1987). The recent volume by Stacey & Koenig (1990) brings together up-to-date accounts of work on cooperative breeders world-wide.

In common with studies elsewhere, the research within the United States provides substantial *prima facie* evidence for habitat saturation as an ecological constraint on the breeding systems of these species. In the case of the Florida Scrub Jay, the birds are limited by the availability of the oak scrub habitat in which they breed. For other species the limiting resources are even more specific. The Mexican Jay requires adequate space over which to disperse territories, but additionally requires reliable access to acorns as an overwin-

tering food. This latter requirement is even more selective in the case of the Acorn Woodpecker, where territories invariably possess special trees used for the storage of acorns. Without such trees within the territory, the breeding group using that territory disappears. In the case of the Red-cockaded Woodpecker, which nests in holes in living pine trees (a resource which can be created anew but only at the cost of very large investment of labour on the part of the birds), the distribution of breeding groups is tightly correlated with the availability of tree holes. The Harris' Hawk is limited by the need to hunt large prey, while in Pinyon Jays a biased sex ratio which leaves males unable to find females in some years promotes helping behaviour (see below).

The involvement of close relatives, often parents and their independent or adult offspring, has been identified in most cooperative breeders. Most species are singular breeders, in which only one pair breeds within the group, but a few species have been identified as plural breeders, with two or more nests within the group territory. Helpers in many species bring food to the nestlings of these nests and may also share service as sentries against the approach of predators. One focus of long-term studies of cooperative breeding has been to investigate the value of such assistance to the parent, primarily in the light of kin-selection theory. Some evidence for this exists: for example, yearling Pinyon Jays leave nonbreeding flocks to become group members only in groups whose nesters are close relatives. Kin-selection theory is an attractive explanation for such behaviour and for the evolution of cooperative breeding, yet wherever documented the effects of helpers on reproductive success have been small. In the Harris' Hawk, Red-cockaded Woodpecker, and Pinyon Jay, the benefits of helpers have been negligible or slight; in the Florida Scrub Jay and in the Mexican Jay have been moderate; and only in the case of the Acorn Woodpecker (and then only in one study population) have the effects been marked.

One of the features of these American studies that has acted

against clearcut demonstration of kin-selection effects has been an over-reliance on observational studies of colour-marked birds, with little experimental work undertaken (Smith 1990). Analysis based on observation alone is confounded with a fundamental problem: in order to have offspring available to return as helpers, the parents have to have been previously successful on at least one occasion. This raises the possibility that parental ability is confounded with the presence of helpers, so the simple observation of increased breeding success on the part of birds with helpers may merely mean that these birds are particularly competent. Experimental investigation is needed to demonstrate that helping rather than parental ability is the source of enhanced reproductive success. Only Brown *et al.* (1982) have published such a study to date, in which their experiment confirmed a positive effect of helping. With group-living birds in a saturated habitat, the potential for investigating ecological and demographic constraints by the wider use of experimental removal of whole groups of breeders is substantial. Hannon *et al.* (1985) have already investigated the effect of breeder removal on the resulting within-group conflict in the Acorn Woodpecker and similar work with jay species is in hand by Stacey and his colleagues. In a mirror image of such experiments, Walters and his colleagues plan to construct artificial nesting cavities in areas unoccupied by Red-cockaded Woodpeckers, to see if they can be induced to switch from competing for existing territories to colonizing the newly created ones (Walters 1990). In addition, if Red-cockaded Woodpeckers are indeed limited by the availability of cavity trees, territories of entire groups ought to disappear if one destroys the cavity trees within the territorial boundaries (Hooper 1983). However, the endangered status of this species makes the deliberate conduct of this experiment impossible, though exploiting natural tree destruction following the transit of hurricanes through the breeding range of Red-cockaded Woodpeckers (below) provides a natural experiment of equivalent value. Increased emphasis on experimental manipulations of these populations is therefore likely to develop quickly, although the risk that experiments interfere with the underlying structure of the population for which perhaps two decades of demographic history have been accumulated is a real one. In one effort to by-pass this problem, Woolfenden & Fitzpatrick (1990) are collaborating with R. L. Mumme in developing a parallel study of Florida Scrub Jays at a site near, but outside, the Archbold Biological Station core population, with the intention of conducting experimental manipulations at the new site. First results from one such manipulation support the notion that help is of net value to the recipient.

Smith (1990) points out that long-term studies of bird populations are developing increased emphasis on the role of individuals within the populations and effectively constitute an extension of behavioural ecology into what might be called social demography. This concept of interaction between demographic constraints and individual behaviour is at the core of Woolfenden & Fitzpatrick's (1984) explanation for cooperative breeding. If juvenile and adult survival is

high, particularly within breeding groups, then offspring may be able to remain in the natal group and defer breeding until a suitable opportunity arises on or near their natal territory. In this way they might postpone or eliminate the costs of dispersal at the price of deferring the start of breeding, but may gain in lifetime reproductive success by so doing. This strategy may also be valuable where recruitment can vary sharply between years, with some cohorts dominating the later population, as shown by Woolfenden & Fitzpatrick (1984) for the Florida Scrub Jay and by Brown (1987) for the Mexican Jay. In many studies of cooperative breeders, the absence of experimental work has resulted in confounding of demographic variables, making it difficult to evaluate the Woolfenden-Fitzpatrick model. Nevertheless, Marzluff & Balda (1990) have shown that in Pinyon Jays those males that help are typically lighter in body weight than those other yearlings that gather in non-territorial flocks. They suggest that these lightweight males may be subordinate and less able to compete for females within these flocks, particularly given the male-biased sex ratio. These subordinate jays might instead return to their natal territories and assist their parents while enjoying better survivorship and a greater chance of either inheriting the natal territory or one nearby. In addition to this type of observation in the Pinyon Jay, the overall characteristics predicted of cooperative breeders—late initial breeding and high first-year and adult survival—are typically seen in cooperative breeders, and sex ratios are also biased in some species, as in the Pinyon Jay.

One of the major unanswered questions from studies of cooperative breeders is the extent to which the primary breeders in the group are solely the parents of the nestlings. The possibility of using DNA fingerprinting to identify parentage uniquely is now feasible (Burke & Bruford 1987) and is being considered for use in cooperative studies. Indeed, this technique might well become useful in all long-term population studies, not merely those of cooperative breeders.

Smith (1990) notes that current understanding of the ecological constraints within studies of cooperative breeding (and, one might add, of all population studies) is limited by a lack of measurements of the food supplies available to birds at the time of lowest food availability. Such measurements are particularly needed for across-species comparisons. New methods, such as the use of doubly-labelled water, might also help to understand the energetic limitations on individuals within these populations.

Another obvious avenue for development is the use of mathematical models of cooperative breeding. Demographic models have been advanced by Emlen (1982a, b) for the general case, and by Woolfenden & Fitzpatrick (1984) and Koenig & Mumme (1987) for the Florida Scrub Jay and Acorn Woodpecker, respectively. Considerable scope exists for the extension of these models into game theory and dynamic modelling. For example, although Florida Scrub Jays show a highly skewed distribution in individual lifetime reproductive success, indicating that some individuals achieve grossly disproportionate representation of their offspring in future generations, a model of the demography of the population

showed that this distribution was no different than would have arisen by chance combination of mean reproductive and survival values (Fitzpatrick & Woolfenden 1989).

Polygamous mating systems

The study of polygamous mating systems has been a second area of sustained population research in the United States. Although polygamy is the mating system of only 2% of all bird species (Lack 1968), a substantially greater proportion of North American species, at least among passerines, are polygamous (Verner & Willson 1969). As a result, the phenomenon has drawn considerable attention in North America, where a model for the evolution of polygyny in birds was developed by Verner & Willson (1966) and Orians (1969). The basic features of the Verner-Willson-Orians hypothesis are fairly well-known: first, there must be substantial variation in the quality of individual territories, and secondly, the extent to which female reproductive success is dependent upon male aid must be influenced by how rich her territory is in food. As a result, some males are able to sequester unusually rich patches of habitat, to the extent that even a second or third female mating polygynously with that male still has access to better per capita resources than she would obtain by mating monogamously with another male holding a poorer quality territory. This holds true even though in the polygynous case she must share or even get no assistance from the male, while in the monogamous case she might obtain all of the male's help: male parental help simply does not compensate for the poorer resource base of the territory available monogamously. The model has been extensively tested in a variety of species, e.g. with Indigo Buntings *Passerina cyanea* by Cary & Nolan (1979), and most of its predictions confirmed. Nevertheless, it continues to draw considerable interest and has been the subject of some studies of the lifetime reproductive success of individuals pursuing different mating strategies.

Sexual selection

Sexual selection in general has attracted much attention from North American ornithologists. Differences in the ecological pressures on males and females are manifest in several ways, among them differences in wintering latitudes and arrival times by the two sexes. Three hypotheses have been proposed to explain these phenomena. These are, first, that intersexual behavioural dominance forces the subordinate sex to migrate further, at greater cost, to avoid competition. Secondly, that sexual differences and physiological tolerance allow the larger sex to survive colder climates and therefore to remain nearer northern breeding grounds. Thirdly, sexual selection might favour those individuals of one sex that arrive earlier, thus leading that sex to winter closer to the breeding grounds in order to have a shorter journey time. Myers (1981) tested these theories in relation to Red Phalaropes *Phalaropus lobatus* and Sanderlings *Calidris alba*. He found no sexual difference in wintering latitude

among adults, but found that first winter male Sanderlings tended to winter further south than first winter females. By comparing these results with data for seven other species, he showed that only the hypothesis of intra-sexual selection favouring earlier arrival of a particular sex was supported by the data.

Such broad brush analysis provides cross-sectional evidence in support of a particular hypothesis, but long-term studies are needed to demonstrate reproductive or survivorship benefits associated with, in this case, intersexual selection. One such study is the work of Oring and his colleagues (Oring & Knudson 1972, Oring & Lank 1982), who have been engaged in a long-term population study of the polyandrous Spotted Sandpiper *Tringa macularia* since 1973, studying a population on a small island in Minnesota. Spotted Sandpipers have a polyandrous mating system in which females engage in resource defence for control of breeding territories and mates, while males provide most of the parental care. Because of this reversal of sex roles, the study has a special opportunity to examine the evolution of sexual selection and polygamous mating systems. As might be expected from the sex-role reversal, female Spotted Sandpipers returned to the breeding ground in spring ahead of males, setting up their territorial boundaries anew before the males arrived. Similarly, inexperienced birds, both males and females, returned later in the season, when initial territorial defence had weakened and the opportunities for new birds to enter the population were greatest. Again, though, females preceded males, as one might expect. This continuing study should yield new insights into the population consequences of this unusual mating system as further data accumulate.

MONITORING

At the outset it is worth noting that American ecologists have a phobia about 'monitoring'. Franklin (1989) puts it as follows: "We often resort to rhetorical handstands to avoid using the word 'monitoring'." This partly reflects the concern that monitoring activities will consume scarce resources in the mindless gathering of data of unproven value. The full story, however, goes beyond that. A component is due, I suspect, to the use of the 'hard sciences', particularly physics, as a role model by such 'soft' sciences such as ecology. The brilliant successes of physics and engineering in the United States in such areas as the development of the atomic and hydrogen bombs and in the exploration of space (*pace* the recent disasters) have given these fields both a credibility and a budget they lack in Britain. This has generated a cultural bias towards regarding these disciplines as the epitome of science. This bias has been reinforced by two developments within ecology. First, the field of ecology, and in particular avian ecology, has been dominated by the work and school of the late Robert McArthur (e.g. MacArthur 1972). His brilliance in devising elegantly simple tests to evaluate predictions from his various theories, particularly competition theory, led several genera-

tions of ecologists to believe, or at least to behave as if they believed, that an elegantly designed test could substitute for a thorough grounding in background natural history. Moreover, the group of U.S. biologists with the greatest training and background in natural history—wildlife managers—are typically found in agencies in which management and administrative responsibilities preclude significant research effort on theoretical issues. Secondly, a series of crucial papers on the methodology of ecology corrected the original bias only by overemphasis on rigorous hypothesis formulation, thus perpetuating the underemphasis of background natural history (see James & McCulloch 1985 for a review of these issues). Both trends have operated against the evolution of long-term studies, both by distorting the education of young biologists and by shaping expectations within the peer review process for grants and publications as to what proper ecological science consisted of.

Since few professional ornithologists involve themselves in sustained natural history studies, such work conducted in the United States has largely been the province of amateurs. As in Britain, many amateurs lack the formal training to encourage them to develop research studies of their own and much of their effort has therefore gone into participating in extensive collaborative studies akin to those organized by the British Trust for Ornithology in Britain. In this way both natural history and bird monitoring activity have come to be associated with being 'amateur', leading many professionals to steer clear of involvement in such work. The two major monitoring programmes in the United States have therefore been conducted either largely as a recreational activity (in the case of the Christmas Bird counts organized annually by the National Audubon Society—see below), or as an administrative task by officials of the U.S. Fish and Wildlife Service (in the case of the Breeding Bird Survey). In fairness, however, it should be noted that several eminent ornithologists and ecologists have drawn on these two surveys in the course of their research (Bock & Ricklefs 1983, Brown 1984, Robbins 1985, Bock 1987), and a new generation of American researchers is continuing this trend (Root 1988, Bart & Klosiewski 1989). Combined with the steady build up of data within the Christmas Bird Count and Breeding Bird Survey schemes, this trend has resulted in considerable current research activity in the use of monitoring data for population studies (Sauer & Droege 1990).

The Breeding Bird Survey is administered by the U.S. Fish and Wildlife Service in association with the Canadian Wildlife Service. A statistically stratified sample of census points ensures systematic coverage of the United States and the southern parts of Canada. The scheme began in 1965 and is dependent upon volunteer cooperators. Each participant covers a BBS route extending along 24.5 miles of secondary roads. At 50 stops, one-half mile apart, the observer conducts a 3-minute count of all birds heard and seen there. The survey of each route starts shortly after dawn and is conducted during the early breeding season, which for much of the United States is June. Standard guidelines are used to control the quality of the data gathered and collated at the

Breeding Bird Survey office at Patuxent Wildlife Research Center, Laurel, Maryland. The scheme gathers information on more than 230 species, with the intention of monitoring changes in the size of breeding populations of these species. The data are typically analysed using a formal statistical procedure developed for the purpose (Geissler & Noon 1981). The results from the first 15 years of the scheme (1965–1979) have been published (Robbins *et al.* 1986).

The Christmas Bird Counts have been conducted since 1900, administered by the National Audubon Society. Volunteers survey a 15-mile diameter circular area within two weeks of Christmas Day. The counts have grown enormously in popularity in recent years, and currently about 1500 circles are surveyed each year. Censusing effort is not standardized and the number of people searching each circle, the manner in which they do so, and the number of hours they spend are not controlled, except that field work is confined to a single day within each individual circle. The actual effort invested in a circle is, however, recorded as the number of party-hours, and in recent years the counts obtained at feeders or through nocturnal searches for owls and the like have been kept separate. Various efforts have been made to devise methods of adjusting the raw counts for differences in effort across sites and over time, the most promising being a method due to Butcher & McCulloch (1991). This method is essentially that devised by Lack (1986) for the British and Irish *Wintering Atlas*.

Data from these two monitoring schemes have been used in a number of ways, discussed under separate headings in the following text.

Range and status changes

One of the advantages of an extensive monitoring programme over a single-site study is that one can detect geographical variation in trends. Extensive long-term population studies such as are provided by the BBS and CBC schemes therefore allow one to follow range changes. Figure 1 illustrates some results from the Breeding Bird Survey. The Loggerhead Shrike *Lanius ludovicianus* has been decreasing over much of the United States, as shown here in the national trend. The bird feeds principally on large insects and on small mammals and it has been suggested that the taking of contaminated prey may account for the decline (Robbins *et al.* 1986). The decline might be aggravated by the loss of the hedgerows that formerly provided nesting habitat. Similar losses of pasture land may also have removed feeding habitat. Butcher & Lowe (1990) have analysed the Christmas Bird Count data for this species and shown that the migrant race is the one particularly affected.

In contrast, House Finches *Carpodacus mexicanus* have been increasing and spreading in the northeastern United States, following the release of birds onto Long Island, New York in 1942 (Fig. 1). However, despite this expansion the numbers of birds recorded per route is still very low, at least relative to the densities prevailing in the western United

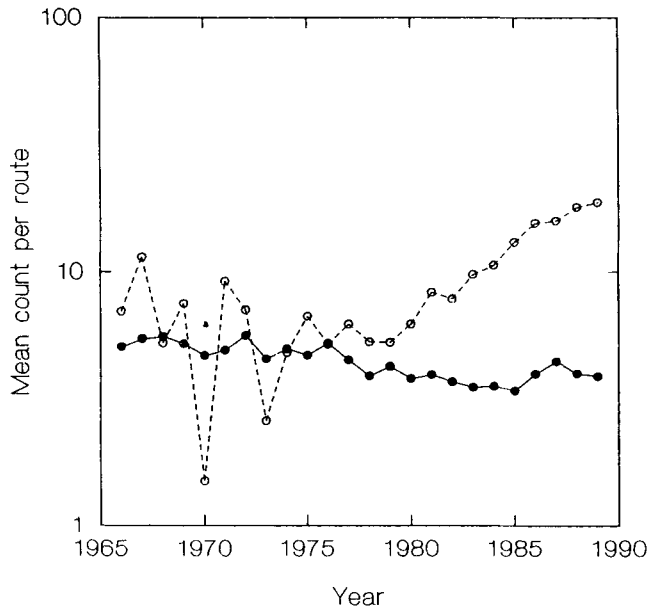


Figure 1. Long-term population trends in the Loggerhead Shrike in the United States (solid dots) and in the House Finch in the northeastern United States (open circles), based on mean count per Breeding Bird Survey route. Here the northeast refers to U.S. FWS Region 5 comprising the states of Connecticut, Delaware, Maine, Massachusetts, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, Vermont, Virginia, and West Virginia.

States. Similar analysis has documented the northward range expansion of the Cattle Egret *Bubulcus ibis*, Northern Cardinal *Cardinalis cardinalis*, and Mockingbird *Mimus polyglottos*, and southward range expansions by Starling *Sturnus vulgaris*, Barn Swallow *Hirundo rustica*, and Cliff Swallow *H. pyrrhonota* (e.g. Robbins 1985).

One of the principal conservation measures available to the U.S. Fish and Wildlife Service is the classification of species as Threatened or Endangered. Once a species achieves such status, the Service is mandated by law to make extraordinary efforts to prevent further decline. However, the enormous cost of such operations has led the Service to develop an early warning system to detect species that could potentially become threatened or endangered. Such warning may enable the Service to take conservation action while populations are still relatively large. To this end the Office of Migratory Bird Management has produced a list of migratory, non-game bird species of management concern, listing species that live in threatened habitats or that have unstable or declining populations (Office of Migratory Bird Management 1987). The list is intended to guide the Service in planning research and conservation measures and in identifying species that warrant further study. Such research includes the commissioning of status reports covering distribution and population trends for individual species. For example, Butcher & Lowe (1990) surveyed the population trends of six species of agricultural birds that appeared in the

list of species of management concern, documenting changes in range and population numbers over a 25-year period. It seems likely that such use of long-term population monitoring studies for status assessment will increase, particularly given the number of decreasing species in the United States (see below).

Environmental changes

The long-term nature of the BBS and CBC data naturally permit their use as indicators of baseline levels and variability of bird populations in the United States. With the long-term accumulation of information, these studies are being increasingly used to study the impact of environmental changes affecting the bird populations of the country.

Most of the migrant species in the eastern United States spend the winter in the neotropics, particularly in Central America. A variety of long-term studies have fairly consistently indicated decreases in the numbers of neotropical migrants on the breeding grounds in the United States, particularly in the eastern deciduous forests (Johnston & Winings 1987, Holmes & Sherry 1988, Terborgh 1989). Two explanations for these declines are possible. First, large-scale destruction of tropical forests might be eliminating the overwintering habitat for these species, reducing the carrying capacity of the wintering grounds and therefore limiting the populations returning to the United States to breed. This would be analogous to the reduction in the mid-1960s of numbers of breeding Whitethroats in Britain and elsewhere in Europe following the drought in the Sahel (Winstanley *et al.* 1974). On the other hand, the North American forests that provide the breeding grounds of these species have been subjected increasingly to fragmentation by road-building, housing, and other developments. As a result the average size of forest patches has decreased far faster than has total forest area. Substantial evidence exists to show that neotropical migrant species breeding around the edges of such woodlots are particularly sensitive to such patch size reduction. Predation and brood parasitism are greatest around patch edges and the effect is aggravated by urbanization: suburbia tends to support higher densities of parasitic cowbirds and of nest predators (Blue Jays *Cyanocitta cristata*, squirrels, raccoons, and so on) than does undisturbed woodland. This is partly because many of these parasitic or predatory species are well adapted to the disturbed habitats of suburbia, but also because some of the species, e.g. Blue Jay, now survive the winter in greater numbers because of the availability of bird feeders in suburban gardens. The net effect is to reduce the density of neotropical migrants and, in some cases, to restrict them to the interior of the forests (Wilcove 1985, Terborgh 1989). Widespread fragmentation of the eastern deciduous forests would therefore reduce the overall numbers of neotropical migrants by reducing the amount of suitable breeding habitat for them. On the other hand, it is also possible to argue that the various long-term census sites demonstrating decreases in numbers of neotropical migrants are themselves not part of pristine forests but are essentially

nature reserves in the midst of ongoing suburban development. If so, the decreases they record in neotropical migrant numbers might be simply due to their increased isolation from sources of immigration by these species, with there being no large-scale overall decrease in neotropical migrant numbers.

Against this background, considerable controversy as to the meaning of long-term population trends in neotropical migrants has erupted in the United States. Conservationists express concern at the drastic declines they perceive while pure scientists validly question whether there might be bias in the censuses indicating declines and whether fragmentation of North American forests rather than tropical deforestation might account for local changes (e.g. Hutto 1988). Robbins *et al.* (1989) have recently drawn on the Breeding Bird Survey results to try to resolve this situation. They showed that over the period 1966–1978 no major differences in population trends were apparent between neotropical migrants and short distance migrants (species migrating but wintering within the United States). Between 1978 and 1987, however, neotropical migrants, but not the permanent residents, showed a statistical preponderance of declines. Moreover, by classifying these species first as users of forests or scrub on their wintering grounds in Mexico and secondly as forest or non-forest species on their breeding grounds in the eastern United States, Robbins *et al.* (1989) were able to differentiate between the effects of fragmentation and deforestation. Species wintering in tropical forests showed more severe declines than did species wintering in tropical scrub, suggesting that destruction of primary forest was a major factor in the decline of neotropical migrants. On the other hand, no differences could be established between species that bred in eastern forests and those that bred in scrub. This latter part of the analysis was, however, limited by the few species that changed their habitat seasonally. Their overall conclusions are, however, supported by broader reviews of the available evidence demonstrating neotropical migrant declines in the United States (Askins *et al.* 1990). Given the conservation importance of the issue, long-term population studies in the United States will undoubtedly continue to address this issue.

Another environmental effect of continuing interest in the U.S. is the impact of agricultural pesticides and other contaminants on the fortunes of bird populations. Since the publication of Rachel Carson's *Silent Spring* in 1962, conservationists have been particularly sensitive to the influence of contaminants on the environment. Despite this, it remains true that the overall control of contaminants in the U.S. is poorer than in Britain, although this situation is changing rapidly. Until recently no attempt has been made to assess the overall impact of pesticides on the fortunes of bird populations in the United States. In 1989, however, my research group at the University of Maine began, in collaboration with Gregory Butcher of Cornell University's Laboratory of Ornithology and with funding from a group of agrochemical manufacturers, a systematic analysis of the BBS and CBC data in relation to information on pesticide use and agricultural

practices within the United States. The scope of this work is essentially similar to that of O'Connor & Shrubbs's (1986) *Farming and Birds*, which drew on the BTO's various bird monitoring schemes' data.

SPATIAL VARIATION AND SCALE

One of the particular values that extensive data such as the Christmas Bird Count provides is that one can examine temporal correlations over a wide geographical distribution, thereby obtaining perspectives that extend beyond those provided by temporal studies at single sites. Kerlinger *et al.* (1985) took advantage of these features of the CBC to derive a conceptual basis for eruptions of wintering Snowy Owls *Nyctea scandiaca* in North America. Observations on owls at individual sites showed that they tended to occur in periodic eruptions thought to reflect a dependence on the cycles of microtine rodents in the tundra. They found that owls reached their greatest abundance in the northern Great Plains and the Midwest regions of North America, but that along the East and West Coasts abundance was one to two orders of magnitude lower and much more variable. Although variations within the East or within the West Coast regions were synchronous, as possibly were variations within the Great Plains regions, fluctuations were not synchronous between these regions and time series analysis showed that the winter invasions were not cyclic. Kerlinger *et al.* (1985) suggested that basing earlier studies on only a small proportion of the continental population of Snowy Owls led to biased impressions of the cyclicity; they suggested, instead, that Snowy Owls are regular migrants over much of the winter range, possibly driven by climatic factors over their breeding grounds.

This question of how the spatial scale of a study influences one's picture of the dynamics of the species of interest is fast becoming one of the most active areas of research in the United States (e.g. Wiens 1981, Maurer 1985, Holmes & Sherry 1988). Bird populations vary substantially from place to place, even within the same habitat. An intrinsic difficulty for long-term population studies at single sites is therefore knowing whether changes recorded there are due to peculiarities of the local site or whether they reflect regional changes. (This problem also arose above in relation to these studies indicating declines in neotropical migrant numbers.) The availability of long-term extensive population surveys, such as the Breeding Bird Survey and the Christmas Bird Count, allow a degree of control for this, permitting site-specific changes to be disentangled from the regional changes. Thus, Witham & Hunter (in press) have drawn on BBS data from sites along a coastal belt from Massachusetts to Maine in order to allow them to recognize whether changes on their study site at the Holt Forest (Arrowsic, Maine) could be attributed to the experimental manipulations of that forest or to other changes in the region as a whole. Similarly, Holmes & Sherry (1988) have examined changes in the abundance between 1969 and 1986 of 19 species breeding at

Hubbard Brook in New Hampshire, comparing changes in abundance recorded on their intensively studied 10-hectare plot in unfragmented forest with the statewide regional trends as reflected in Breeding Bird Surveys. They found that 12 of the 19 species (mostly forest-living migrants) showed similar trends at both levels, two-thirds of them showing stable populations and the other four decreasing significantly. The other seven species varied in the patterns shown. Statistically significant changes were more frequent within their study site than within the state as a whole (eight decreasing species vs five, with only one species increasing). Their detailed data on food abundance and on vegetational changes associated with forest succession suggested that most of the declines were induced by conditions on the study site, the one exception being a group of short-distance migrant or permanently resident species whose populations varied with the extent of winter mortality from year to year. They found in particular that the abundance and availability of lepidopteran larvae significantly affected the frequency of renesting, the incidence of secondary attempts, and nesting success as reflected in nestling starvation, growth rates, and fledging success. The decline of several bird species was associated with the gradual disappearance of defoliating caterpillars that had erupted on the site in the early years of the study. Such eruptions are relatively frequent in the area, but do not occur in synchrony across the state. As a result, the regional changes were little affected by this type of decrease, in contrast with the local trends.

Wiens and Rotenberry in particular have conducted extensive long-term studies of the birds of shrubsteppe habitats in the United States and found that many of the patterns they observed were inconsistent with concepts of equilibrium community dynamics (Wiens & Rotenberry 1979, 1981, Rotenberry 1980, Rotenberry & Wiens 1980, 1981). When data from small-scale study plots were pooled, however, variation in population densities were greatly reduced, as also shown by the long-term study at Hubbard Brook by Holmes and his colleagues (Holmes *et al.* 1986). This pattern could either be because regional scale studies average out variations that occur at the local study site, or it could be due to the small study plots constituting essentially samples of the true biological patterns, with the fixed boundaries of a study plot sampling different proportions of a population that redistributes itself from year to year within the larger regional scale boundaries. While this latter can be handled by suitable choice of size of sampling area, at least within limitations imposed by available logistical support, the former is more troublesome. In principle, the aggregated results from smaller subplots will yield an ever closer approximation to the 'true' underlying regional dynamics, but the loss of resolution involved may be detrimental to scientific understanding. Habitat is typically distributed in patches across the landscape, with not all patches of equal value to birds. As growing theoretical work has shown, the resulting population dynamics may depend on the characteristics of this landscape (Urban & Shugart 1986). If some patches are preferred habitat for a species, while other patches are less preferred,

the overall dynamics of the population will depend on the spatial distribution of these patches. Understanding the reasons behind regional differences in bird population dynamics may therefore require a knowledge of the interpatch dynamics. For example, when primary habitats are saturated, secondary habitats are often colonized, and when these are in turn colonized fully, further habitats come into use (Fretwell & Lucas 1969, O'Connor 1986). Hence primary habitats will be usually saturated and will vary little from year to year, but secondary habitats will vary substantially. In extreme cases, even 'sink' habitats may be colonized, as birds utilize superficially attractive habitat, but experience inadequate reproductive success to offset mortality there (Van Horne 1983). According to these ideas, local patch dynamics are linked to population variation at a larger scale.

Considerable interest is developing in such patterns of natural variability of populations, both in space and time, reviewed in a non-ornithological context in the papers in Pickett & White (1985). Wiens (1990) points out that there are four views of community equilibria: (a) most communities are fully saturated with species and in a steady-state diversity; (b) bird communities are not in a steady-state equilibrium but form a dynamic equilibrium, with numbers tracking environmental resources by behavioural, distributional, and demographic adjustments; (c) resource variations are not closely tracked but populations in communities are strongly affected by episodic 'environmental crunches', periods of severe climatic or resource limitation interspersed with more benign periods of abundant or superabundant resources; and (d) species abundances are rarely, if ever, determined by resource levels, with communities being essentially non-equilibrial, often not necessarily due to stochastic factors. Wiens also points out that the frequency of 'unusual' conditions (drought years, severe winters, and so on) are more frequently cited in short-term studies than in long-running population studies. That is, a relatively small change from one year to another is seen as involving an unusual event within the time horizon of a short-term study, but the same change is more frequently seen as part of natural background environmental variability when viewed in the context of a longer run of years.

Perceptions aside, the use of different temporal scales of study may reveal processes hitherto undetected. Most North American birds have pronounced annual cycles of behaviour linked to the annual seasonal changes in their environment, but for others a longer term component is present. Spruce budworm specialists such as the Cape May Warbler *Dendroica tigrina* enjoy better breeding conditions when at the peak of a budworm outbreak, and population levels correspondingly increase following outbreaks. Levels then decline slowly as reproductive output decreases, and mortality rises, as the outbreak wanes in later years. In any single year, then, warbler numbers are not equilibrial, yet over periods large enough to encompass reliably a budworm outbreak population level may be equilibrial. Similar population stability with long period observation units probably characterizes the numbers of irruptive species and of raptorial species that feed

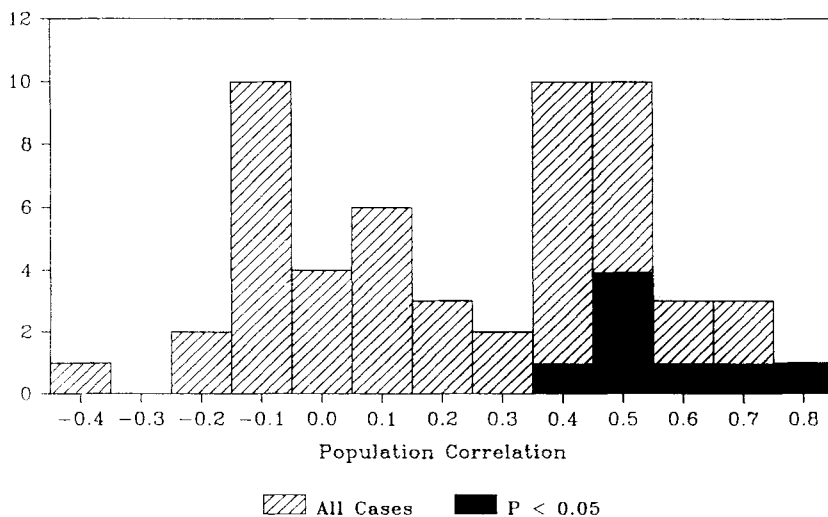


Figure 2. Frequency distribution of correlations of population sizes in sparrow populations wintering in southern Arizona with rainfall there the previous summer. Based on data in Dunning & Brown (1982).

on cyclic rodents. Taylor & Woivod (1982) have shown that British bird distributions have species-specific scales of variation both spatially and temporally, and some unpublished analysis indicates that this is true also of North American birds (R. J. O'Connor and R. B. Boone unpubl.). Although little discussed in the literature, any temporal scaling of this type has major implications for the dynamics of each species (McArdle *et al.* 1990).

Noon *et al.* (1985) attempted to evaluate the natural variability of North American bird populations empirically. They assessed annual population densities for a range of study plots distributed over the United States and found relatively weak differences between habitat types or along geographical gradients, though with substantial variation within all habitat types. Since environmental unpredictability and severity appear to be associated with variation in bird communities, this lack of latitudinal gradients in variability within North America may indicate that climatic conditions are less directly associated with latitude in North America than was found to be the case in Scandinavia (Järvinen 1979).

Environmental variability seems to be particularly important in arid regions within the United States. Pulliam and his colleagues (Pulliam 1985, Pulliam & Dunning 1987) suggested that summer rainfall regulated the density of sparrows (i.e. emberizids) in the region by determining the extent to which grasses were able to develop and sprout, thus making seeds available for wintering sparrows. Figure 2 shows a general tendency for wintering sparrow populations to be correlated with summer rainfall. Note, though, that despite the bias towards positive correlations, a significant number of species-plot correlations are centred on zero values. That is, even within a single region, not all populations at all localities responded to rainfall in the same way. In keeping with this, Laurance & Yensen (1985) conducted a similar analysis for the sparrow populations they were studying in the northern Great Basin, but found no such relationship. Hence, even

though a tracking of environmental resources can be documented for some populations in some places, the phenomenon is by no means universal even within a given taxonomic group.

SLOW OR EPISODIC PROCESSES

Bird populations are widely assumed to live in an equilibrial world, so that a study conducted at any time or at any place portrays the steady-state condition of the populations involved. Deviations from these conditions are, at best, regarded as stochastic, with no long-term effects on population levels. In reality, however, the environmental conditions in which birds find themselves may be subject to long-term changes of two types (Franklin 1989). First, conditions may alter slowly relative to the lifetime of individual birds, as with succession or climatic amelioration. Secondly conditions may change dramatically following rare but statistically certain episodic events. Hurricanes, volcanic eruptions, and current shifts in the ocean constitute events of this type. Acquiring an understanding of the effects of these changes on bird populations inevitably requires multi-year study at fixed plots, i.e. sustained longitudinal studies.

Johnston & Odum (1956) conducted one of the classic studies of breeding bird populations in relation to plant succession, but did so by means of a space-for-time substitution: ten 20-acre areas in the secondary upland sere of the piedmont region of Georgia were censused for breeding birds, with the ten areas representing successional stages covering the transition from grassland through shrub land and pine forest to hardwood (oak-hickory) forest. They found that breeding bird densities increased from 15-40 pairs/100 acres in recently abandoned fields to 228 in a young oak-hickory stand, though with lower densities than expected in the young pine forest. This type of study provides a broad indication of the response of birds to successional change, but

requires long-term studies to confirm the validity of space-for-time substitution.

One such longitudinal study has been reported recently by Raphael *et al.* (1987). They compared breeding bird censuses performed on a Sierra Nevada forest plot burned in 1960 and censused (together with a control plot) over the period 1966–1983. They found a general increase in bird numbers on the burned plot as successional changes progressed, with canopy-feeding birds especially increasing as a forest canopy developed. Primary cavity nesters decreased over the first few years as the dead trees left after the burn were lost. Their study also indicated that some systematic increases in individual species populations took place on the control plot, despite a relatively constant foliage volume. The species involved in this—Yellow-rumped Warbler *Dendroica coronata*, Nashville Warbler *Vermivora ruficapilla*, and Western Tanager *Piranga ludoviciana*—were different species than those increasing on the burned plot. In a space-for-time substitution, such increased densities would have been attributed to successional change.

Concern about such artifacts lies behind support from the National Science Foundation for a series of Long-Term Ecological Research (LTER) sites (Callahan 1984, Franklin 1989). This programme provides a six-year commitment of core support for research on selected long-running ecological study sites, with the prospect of similar long-term renewals of satisfactory programmes. The initial programme provided for a network of 20 such sites, each representative of major ecosystems in the U.S. (Callahan 1984). Inevitably, not all ecosystems are represented, nor is there any duplication of plots within ecosystem type, but the programme nevertheless encourages the availability of reference sites for comparison of changes observed in cross-sectional studies. Although choice of methods within each LTER site is the prerogative of the researchers there, the sites share a common emphasis on studying basic ecological processes such as energy and nutrient flow and the role of episodic events in shaping community structure. Such background inevitably informs associated bird population studies in interpreting long-term data. Of the current LTER sites, that at Hubbard Brook, New Hampshire, the site of the studies by Holmes and his colleagues (e.g. Holmes *et al.* 1986) is probably the best known ornithologically.

Weather

Although weather is usually regarded merely as a transient influence on bird populations, there is growing appreciation of the long-term effects of certain types of weather events. Hurricanes can destroy significant components of the habitat needed by individual species, thus imposing a long-term decrease on the carrying capacity of the environment for these species. Engstrom & Evans (1990) describe how three major storms in the course of late summer and autumn 1985 imposed major damage on Red-cockaded Woodpecker cavity trees in an old-growth, longleaf pine forest in southern Georgia. This species uses trees in the size class 30–70 cm

dbh. Under normal conditions their availability is fairly stable: only 2.7% of these trees died in a 4-year period in the study forest in Georgia. During the storms of 1985, however, 24% of the cavity trees were destroyed and a further 12% suffered heavy damage. Even more severe damage was caused to the Francis Marion National Forest in September 1989 when Hurricane Hugo passed through the forest. The extensive loss of trees of all sorts that resulted was accompanied by major reductions in the breeding populations of the Red-cockaded Woodpecker there (F. C. James, pers. comm.). There has been surprisingly little documentation of the long-term effects of such episodic events, but there is a growing appreciation of the need to study such events, partly stimulated by the relative closeness in time of such events as the Mount St. Helens eruption, the Pacific El Niño, Hurricanes Agnes and Hugo, and the Yosemite fires of 1988.

Fire

Fire is another natural phenomenon that imposes episodic disturbances on bird habitat. Some species, such as the Red-cockaded Woodpecker, seem to need periodic fires to come through their breeding habitat if this is to be maintained in suitable condition (Ligon *et al.* 1986). Such responses are probably primarily indirect and due to the effect of fire on habitat, though the direct importance of fire in maintaining open areas for feeding may be significant for some species. Only sustained population studies can reveal such effects.

Birds do not always respond to episodic events such as fires with immediate population changes. Best (1979) found that populations of Field Sparrows *Spizella pusilla* responded to changes in their habitat structure brought about by range fires only some years after the passage of the fire. Similarly, Rotenberry & Wiens (1978) found that Sage Sparrows *Amphispiza belli* also showed delayed responses to the passage of fire through their breeding sites. Such lags are often driven by site fidelity, individual adults tending to return to former breeding sites despite deterioration in the quality of those sites. Nevertheless, the effects can be detected only when a population study has continued sufficiently long to accommodate the lag. A significant body of theoretical and empirical work has developed to accommodate the impact of these kind of lags on the dynamics of bird populations (e.g. Pimm 1984), but the possibility of lags is rarely adequately considered in ecological studies. Long-term population studies offer the necessary raw material for their study and the topic seems set to develop further.

OVERVIEW

This short review of some of the most active long-term population studies in the United States emphasizes four points. First, virtually no study developed as a species study *per se*. Even the most thorough of the population studies described were started with the intention of using the species as a test bench on which to investigate a particular concept

such as cooperative breeding or the nature of mating systems. As these studies have developed, however, they have in several cases contributed to other areas of population ecology, by providing data on lifetime reproductive success, for example. Such widening of horizons is likely to continue within these studies. Secondly, a full appreciation of the value of monitoring data in addressing ecological problems has been slow to develop but is now a growth point in population work within the U.S. This may be particularly significant in the U.S. given the continental scale of climatic and physiographic patterns there. Thirdly, this same range of climate and physiography, and the extremes that go with it, have encouraged a greater appreciation of the significance of episodic events such as fire, hurricanes, and drought, in shaping the destiny of populations. Finally, the sheer scale of North America has led to growing consideration of the consequences of study scale for the perception of population dynamical patterns. These four trends seem likely to shape the immediate future of long-term population studies within the United States.

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